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A STUDY ON THE STRUCTURE OF THE EGG OF THE WALKING-STICK, DIAPHEROMERA FEMORATA SAY; AND THE BIOLOGICAL SIGNIFCANCE OF THE RESEMBLANCE OF PHASMID EGGS TO SEEDS.*

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(With Plate IX.)

A detailed description of the eggs of the walking-stick is essential because in the systematic work on the Phasmidae, the eggs are said to be a very valuable auxiliary means of identification, since their form, "für die Genera charakteristisch ist." (Brunner von Wattenwyl†). Kaup (8) even remarks, "Vielleicht wird man später die Arten durch die Eier schneller unterscheiden lernen als durch die Thiere selbst!"

Measurements of Eggs: Heymons (6) found with Bacillus rossi that the size of the eggs is not constant. "Es sind mir Eier zugekommen, wahrscheinlich die letzten, welche das Weibchen abgesetzt hat, die höchstens die Hälfte der üblichen Grösse besassen, trotzdem waren sie aber normal gebaut und es sind aus ihnen ebenfalls Larven ausgeschlüpft." In Diapheromera femorata a considerable variability in the dimensions of the eggs is also present but the smaller eggs were not necessarily the last ones which the female lays,—they may appear among the first or at any time during the egg-laying.

The size of the eggs varies between the following dimensions:

Length	20–29 mm.
Depth, from dorsal to ventral surface	11–18 mm.
Width or thickness from side to side	9–14 mm.

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† Paper not accessible. Quoted from v. Brunn's (2) paper.

The majority of eggs varied between the following dimensions:

Length	25–29 mm.
Depth	15–17 mm.
Width	12–13 mm.

Shape and Color of Egg: The eggs resemble very small beans with some variation in shape; some are ellipsoid, others ovoid and still others nearly spherical in form. Their color is usually a glossy black, except on the slightly more convex side which is white; instead of the black, however, there may be light shades of gray or light chocolate-brown. Out of a thousand eggs, twelve showed the light shades of gray and only three, the light chocolate-brown color.

When the operculum is removed the egg, in this region, is obliquely truncate and surrounded by an elliptical or oval rim. On the inner margin of this rim rested the operculum. The rim is provided with a circle of yellow, chitinous, bristle-like projections. In most eggs the white color of the slightly more convex side is continued around the base of the rim as a white line.

Operculum: The operculum (Fig. 1, *op*) fits perfectly within the rim of the egg capsule (Fig. 1, *ri*) and is usually set free when the egg is broken. If the operculum is cleared, mounted and examined under the microscope a ragged membrane is discernible at its margin (Fig. 3, *vi*). This is the torn, so-called "shell membrane" to which the operculum was attached.

Sharp (16) who has described a number of Phasmid eggs, has probably overlooked the fact, that the operculum is attached to the so-called "shell membrane." He writes, the operculum "is present in all known eggs of the Phasmidae; it is a lid that fits very accurately to the truncate anterior extremity of the egg: its margin is surrounded by a margin of the capsule, and it is owing to the perfect fit between the two that the operculum retains its position." Müller (13), however, in the case of *Phasma ferula* claims that, "Am Rande des Ausschnitts springt die innere Schalenhaut etwas vor, ein Rudiment der Verbindung der Schale mit dem Deckelchen. Die innere Haut des Deckelchens und die innere Haut der Schale sind also an dem unverletzten Ei ein Continuum." Leuckart (10) who has worked on the structure of the eggs of two species of Phasmids belonging to different genera also finds that, "Durch Hülfe dieser Schalenhaut wird der Deckel, der sonst vollkommen isolirt ist, in seiner Lage erhalten und befestigt."

A number of zoologists who have worked on the structure of the eggs of the Phasmidae claim that a "shell membrane" exists within the inner surface of the chorion. Müller (13) writes, "Die innere Fläche der Schale wird von einer sehr dünnen häutigen Lamella, *der Schalenhaut*, überkleidet, die sich nur in kurzen Stücken von der Schale selbst wegnehmen lässt." Leuckart (10) agrees with Müller that a "shell membrane" lines the inner surface of the chorion. "Dazu kommt als Bekleidung der innern Chorion-fläche noch eine eigne dünne 'Schalenhaut,' die schon von J. Müller aufgefunden ist, also wahrscheinlich unter den Phasmoden eine ziemlich allgemeine Verbreitung hat, obgleich sie den übrigen Insekteneiern abgeht." In the eggs of Diapheromera femorata the so-called "shell membrane" is the innermost layer of the chorion, which peels off in small fragments in the eggs that are in the early stages of development, but in the later stages, as Leuckart (10) has observed, "Bei *Cyphocrania* lässt sich diese Haut ohne grosse Schwierigkeiten in continuo abheben —bis auf die Narbe, an der dieselbe fest mit dem Chorion verwachsen ist und ein weisses Aussehen hat." To Leuckart's observation may be added, in the case of the eggs of Diapheromera femorata, that a firm attachment also exists at the rim between the so-called "shell membrane" and the next outer layer of the chorion.

A microscopical examination of the operculum from the outer surface shows a resemblance to the framework of a dome, which is shut off at the base by a slightly concave floor of chitin. The framework consists of brownish, irregularly-flattened, chitinous rods. All of these rods arise from an elliptical or oval brownish rim of chitin (Fig. 3, *br*) which is in continuation with the similarly colored upper surface of the floor of the dome (Fig. 4, *e*). Some of the rods anastomose, enclosing a large, more or less, central space at the top of the dome (Fig. 3, *c*) and a varying number of irregular areas (Fig. 3, *d*) which are not constant in number in the different opercula. Those rods which do not extend to the top of the dome project free into the irregular spaces (Fig. 3, *p*).

Various authors have called attention, in different Phasmidae, to the resemblance in the histological structure of the egg capsule to the structure of certain plant tissue. Murray (14) finds, "a most striking resemblance to a piece of honey comb" in the structure of the egg capsule of *Phyllium Scythe*. Accord-

ing to Joly (7) who has worked on the structure of the egg of *Phyllium crurifolium* "ce tissu présente la plus grande analogie avec celui du liège, c'est-à-dire qu'il est formé de cellules irrégulières (carrées, pentagonales, sexagonales) très petites et très serrées. La couche extérieure qui recouvre cette coque, est beaucoup plus épaisse et, comme nous l'avons dit, elle ressemble à l'ecorce rugueuse du Chêne-liège, dont elle a la légèreté. Nouvelle et curieuse analogie de notre insecte avec le règne végétal: analogie qui devient plus complète encore, quand on songe que l'oeuf du *Phyllium* est muni d'un opercule qui s'ouvre lors de l'éclosion, à la manière d'une pyxide." Brongniart* who has examined the eggs of Phyllium pulchrifolium also compares the external envelope to that of cork. According to Henneguy (5) who has also worked on the histological structure of the egg-capsule of Phyllium crurifolium, "L'ensemble de la couche externe présente une grande analogie de structure avec la partie libérienne d'une écorce de dicotylédone traversée par les rayons médullaires."

A cross section through the operculum of the egg of Diapheromera femorata shows that the space between the floor and top of the dome is partially filled with chitinous deposits, which, according to a vegetable histologist, resembles somewhat the thin walled parenchyma of plant tissue, except that no middle lamella was discernible (Fig. 4, *a*). Müller (13) describes the chitinous deposition as "ein zelliges Gewebe aus deutlich sechseckigen oben offenen Zellen bilden. Dies scheint einer besonderen Beachtung werth, da die Erscheinung eines regelmässigen zelligen Gewebes in der Organisationsstufe der Insecten gewiss die seltenste ist." It would be rash to speculate as to the formation of this chitinous deposition since the manner in which the operculum is formed is obscure. Sharp (16) suggests two methods: "first, autotomy of the pole of the egg; second, adhesion of the mass of matter from the adjacent nutrient chamber, to form as it were a very imperfect second egg."

"*Hilar area, cicatricula or Narbe*" of *Egg:* On the outer surface of the exochorion, of the slightly more convex side of the egg is an elliptical region resembling somewhat the hilum of a seed. Sharp (16) calls this region the "hilar area," Müller (13) the "cicatricula" or "Narbe," Leuckart (10) and Heymons (6) also use the term "Narbe." The margin of this "hilar area"

* Paper not accessible. Quoted from Henneguy's (5) paper.

is slightly elevated and buff-colored (Figs. 1 and 8, *m*). At the posterior end, this margin narrows enclosing a semicircle (Figs. 1 and 8, *s*) within which lies the micropylar orifice (Figs. 1 and 8, *o*). The margin of this semi-circular area is in continuation with a ridge which extends towards the posterior pole of the egg. The buff-colored ridge joins a triangular extension of the black region of the egg (Fig. 1, *r*) and gradually disappears as it passes posteriorly into the surrounding black surface. Within the slightly elevated buff-colored margin is a white convex region which terminates at the posterior end in the microypylar orifice, where the white color gives way to black (Figs. 1 and 8, *o*).

Mycropylar Apparatus: Müller (13) did not understand how eggs of insects with a hard chorion were fertilized and he takes an extreme view as to the way this phenomenon takes place in the eggs of the Phasmidae. "Bei den *Phasmen* hat die Samenkapsel ausser ihrer einen Oeffnung nach aussen keinen besondern Ausführungsgang. Aber der Eingang der zweihörnigen Samenkapsel liegt gerade über dem länglichen Ausgang des Eierganges. Der Samen tritt also aus der Eingangsöffnung der Kapsel unmittelbar in der Mündung des Eierganges ein, um sofort zu den Eierleitern und Trompeten zu gelangen."

"Wir haben aber bewiesen, das eine Befruchtung der Phasmeneier nicht anders, als vor ihrer Ausbildung und namentlich vor der Ausbildung der Schale, möglich sey."

The micropylar apparatus is very remarkable and differs from any of those which Leuckart (10) has described for so many insect eggs. As already mentioned the micropylar orifice is found at the posterior end of the convex area, just within the space enclosed by the semicircular chitinous thickening of the margin. This opening leads into a small canal, the micropylar canal, which passes a short distance towards the anterior pole of the egg. The micropylar canal is elliptical in cross section and surrounded by extremely thick chitin (Fig. 5, *g*). When the inner surface of the "hilar area" in the region of the micropylar apparatus is examined under a microscope, an invagination of the inner surface of the chorion is readily seen; at the bottom of this inpushing is the opening of the micropylar canal (Figs. 6 and 8, *i*). If the vitelline membrane in this region is now examined under a binocular, one finds that a small, obliquely-inclined, membranous tube has been torn away from the opening of the canal (Fig. 2, *t*). A glance at Fig. 7, *v*, shows the opening

of this membranous tube, the vitelline membrane micropyle, into the vitelline membrane. The sperm thus enters the micropylar orifice, passes through the micropylar canal, then through the membranous tube and out of the vitelline membrane micropyle to reach the egg.

Müller's (13) supposition that the sperm passes from the seminal receptacle, through the common oviduct, then into the oviducts to the ovarian tubule and fertilizes the egg before the chorion is formed is entirely erroneous. Leuckart (10) from observations on Gomphocerus found that the micropyles, "nicht von Anfang an dem Chorion zukommen, sondern erst nach der Ablagerung desselben durch Resorption ihren Ursprung nehmen * * * * . Eine Bestätigung dieser Beobachtung finde ich darin, dass ich nicht selten (wie u. a. bie Borborus, Tetanocera und verwandten Fliegen) Eierstockseier antraf, deren Micropylapparat noch ohen Oeffnung war, sonst aber bereits vollkommen entwickelt schien."

"Vor der Ablagerung des Chorions habe ich an der Dotterhaut niemals eine Micropyle wahrgenommen * * * * . Wohl aber habe ich Fälle beobachtet, in denen bei Anwesenheit der Chorionmicropyle die Dotterhaut noch ohne Loch zu sein schien." In all probability the eggs of the walking-stick are fertilized as they pass below the opening of the seminal receptacle.

The Biological Significance of the Resemblance of the Phasmid Eggs to Seeds: A number of naturalists have called attention to the striking resemblance of the Phasmid egg to a seed. In some cases, the egg resembles the seed of the natural food plant of the insect.

In seventeen species of Phasmids obtained from Lifu and New Britan, Sharp (16) has described the eggs of a number of these. In regard to the resemblance of the eggs to seeds he writes: "The climax of the peculiarities is found in the extremely perfect structure of their eggs and the resemblance of these eggs to seeds. The egg of the Phasmid has not only a general resemblance in size, shape, colour, and external texture to a seed, but the anatomical characters of certain seeds are reproduced on the external surface, there being a hilar area, a hilar scar, and a capitulum corresponding to the micropylar carunele of such seeds as those of the Castor-oil plant (Ricinus communis). The hilar area on the inner surface of the capsule is, in shape, like the embryo of a plant. Moreover, naturalists who have examined these eggs

declare that the minute structure of this curious egg-capsule cannot be distinguished histologically from plant-structure."

Among the leaf-insects the resemblance of the eggs to seeds is especially marked. Nab* as early as 1854 has compared the egg of one of these leaf-insects to the seed of the "Belle-de-Nuit (*Mirabilis Jalapa*)." Henneguy (5) in the case of the egg of Phyllium crurifolium claims that, "Sa forme est celle d'un akène d'Ombellifère, et représente, par example, la moitié d'un jeune diakène de *Conium maculatum*. L'oeuf diffère de l'akène d'Ombellifère en ce que son opercule régulièrement conique, est situé au centre de sa face supérieure, tandis que le style conoïde de l'akène est aplati sur la face commissurale." Morton (12) in this same species writes that the "egg has been confused with a seed of Mirabilis and Coniom!"

According to Stockhard (18) the walking-stick, Aplopus mayeri, is found only on its food plant, *Suriana maritima*. "While one may find a close resemblance in size and color between the eggs of *Aplopus* and the seed of *Suriana*, both of which fall from the branches to the ground, where they are obscured among the débris" yet the eggs differ from the seeds considerably in shape.

The eggs of Diapheromera femorata were shown to a number of botanists, and with one exception, all mistook them for seeds. The botanist who did not fall into this error broke the egg before giving his opinion. When asked as to what seed the egg resembled all failed to recall any particular one. A leguminous seed, such as a small bean, was suggested, but none could be found in the natural habitat of Diapheromera, that resembled its egg in size and color.

If these botanists are unable to distinguish the egg of a walking-stick from a seed, can a grain-eating bird distinguish between the two? If a bird were to feed on the seeds of the Suriana maritima which resemble the eggs of Aplopus mayeri in size and color, could the bird discriminate between the two, on account of a difference in shape?

Goldi (4) in the case of the eggs of two Brazilian walking-sticks raises the question as to how far this imitation is useful in the protection of these eggs. Grain-eating birds may eat the egg but general insectivorous birds would probably mistake it for a seed and leave it untouched. The protective dress of the

* Quoted from Henneguy's (5) paper.

egg may be only a relative protection in which new dangers are involved. He next raises the argument that these eggs on account of the resemblance to some Brazilian seeds, deceive, so he believes, the egg-parasites.

This would imply that through the sense of sight the egg-parasite would overlook the eggs on account of their resemblance to some Brazilian seeds. It is open to serious question whether the egg-parasites are guided to the eggs of their host through the sense of sight alone, if at all. One illustration will suffice. We (15) have found that Trichogramma pretiosa parasitizes the eggs of Cimbex americana, and yet the egg-parasite cannot see the eggs of its hosts as Cimbex deposits its eggs in a receptacle within a willow leaf. In all probability, the sense of smell plays an important role in guiding the egg-parasites to the eggs of their hosts.

A careful survey of the literature shows that the eggs of Phasmids are subjected to the attack of a number of enemies. According to King (9) the eggs of Anisomorpha buprestoides "are victimized in a similar manner by a minute species of Ichneumon fly, one of which has fortunately been obtained; it is probably one of the Chalcididae: all the transformations take place within the egg, and when fully developed the perfect Ichneumon fly emerges therefrom."

Bates (1) "observed that the author of the note was probably in error in attributing the name of Anisomorpha buprestoides to the species in question, which seemed to be a true Phasma."

Smith (17) "remarked upon the peculiarity of all the transformations of the Chalcidite parasite taking place within the egg of the Phasma; such a mode of development was novel, if true, but he suspected some error of observation."

M'Lachlan (11) "suggested that the cocoon of the Chalcis had been mistaken for the egg of the Phasma."

von Brunn (2) records the observation of Wolff von Wülfing, that the young larvae as well as the eggs have many enemies, "hauptsächlich Springspinnen und Hauseidechsen."

Girault (3) in his paper on the "Hosts of the Insect Egg-Parasites in North and South America" does not record an egg-parasite from any Phasmid.

I think that the resemblance of the eggs to seeds has no biological significance as a means of protection against the egg-parasites, if the eggs of the Phasmidae are parasitized. Sharp (16)

in all the species which he has examined believes that these resemblances in the eggs have no bionomic importance for the species and I am strongly inclined to accept his view in the case of the egg of Diapheromera femorata.

I am indebted to my teacher and friend, Prof. Wm. S. Marshall, for many valuable suggestions in this work and the more than ordinary courtesies extended to me in the use of his excellent entomological library.

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Explanation of Plate IX.

All figures were drawn with a camera lucida.

Fig. 1. "Hilar area" on the slightly more convex side of the egg *op*, operculum; *r*, rim in which the operculum fits perfectly; *m*, margin of the "hilar area"; *s*, semicircular margin; *r*, buff-colored ridge which passes over into the triangular extension of the black region of the egg; *o*, micropylar orifice.

Fig. 2. Vitelline membrane of egg, after the chorion of the "hilar area" has been removed. *t*, membranous tube, which connects with the opening of the micropylar canal on the inner surface of the chorion.

Fig. 3. Operculum from the outer surface. *vi* torn so-called "shell membrane" to which the operculum was attached; *br*, brownish rim of chitin from which the irregularly-flattened chitinous rods arise; *c*, large, more or less, central space at the top of the operculum enclosed by the anastomosing rods; *d*, irregular areas which are not constant in number in the different opercula; *p*, rods which project free into these irregular spaces.

Fig. 4. Cross section of a part of the operculum; *e*, brownish upper surface of the floor of the operculum; *a*, chitinous deposits, between the floor and top of the operculum, resembling somewhat the thin-walled parenchyma of plant tissue except that no middle lamella is discernible.

Fig. 5. Cross section of the micropylar canal *g*, which is surrounded by extremely thick chitin. This canal opens to the exterior by the micropylar orifice.

Fig. 6. Posterior region of the inner surface of the "hilar area" of the chorion; *i*, opening of the micropylar canal in an invagination of the inner surface of the chorion; *o*, micropylar orifice.

Fig. 7. Vitelline membrane in the region of the micropylar apparatus; *i*, opening of the membranous tube, the vitelline membrane micropyle, into the vitelline membrane.

Fig. 8. "Hilar area" on the outer surface of the exochorion; lettering as in Figs. 1 and 6.